

BIOLOGICAL OBSERVATIONS ON *XENOGLOSSA*
FULVA SMITH WITH SOME GENERALIZATIONS
ON BIOLOGICAL CHARACTERS OF
OTHER EUCERINE BEES
(Hymenoptera, Anthophoridae)¹

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The Eucerine bees of the genera *Xenoglossa* and *Peponapis* are of interest because, in so far as reported, the species collect pollen solely from plants of the genus *Cucurbita*. Although each of these bee genera is represented in the United States by two or three species (some rather wide ranging), apparently nothing has been recorded of their nesting habits and behavior. The observations presented here, while limited, are offered as a fragmentary contribution to the knowledge of *Xenoglossa*.

The species of *Xenoglossa* (and *Peponapis*) appear to have considerable importance in the pollination of wild and cultivated cucurbits in various parts of Central and North America. The introduced honeybee, *Apis mellifera* Linn., when reasonably abundant, visits flowers of *Cucurbita* in numbers, but it does not seem to have replaced the native species of bees, even in the more northern portions of their range. Furthermore, in areas where commercial beekeeping is not practiced, or where conditions are unfavorable for the maintenance of populations of escaped honeybees, or where other plants are more attractive to the honeybee, species of *Xenoglossa* (and/or *Peponapis*) may be the only bees visiting cucurbit flowers in any significant numbers.

LOCALITY AND NESTING SITE

Observations were made on August 18 and 19, 1954, in Mexico, at a campsite 11 miles southwest of Acambaro, Guanajuato, and 3½ miles northeast of Zimapecuaro, near the border between the states of Guanajuato and Michoacan. The elevation is approximately 6,900 feet.

¹This one of a series of studies on the habits of anthophorid bees in Mexico made possible by a grant-in-aid from the Associates in Tropical Biogeography, University of California.

The general area around Zinapecuaro receives its major rainfall from June through September. Much of it occurs in heavy downpours, generally during the afternoon or at night.

Remnants of the original vegetation indicate that it was once on the margin of the oak scrub. To the south, east, and north the landscape slopes gradually upward to tree-covered hills. However, in the camp area and for a considerable distance to the west, the land is cultivated intensively. Planting is largely restricted to *milpas*, consisting of alternated corn, beans, and squash, and these were present in all directions from camp. The closest area was about 150 feet west of the nesting site across a small arroyo (Plate 36, upper fig.).

In the area, honeybees were definitely scarce, and the individuals seen were at flowers other than *Cucurbita*. The *Xenoglossa* and *Peponapis* appeared to be present in sufficient numbers to clean the cucurbit flowers of pollen in the very early morning before the honeybees became active. Whether this accounted for the absence of honeybees from these flowers or whether some other factor was operating, was not determined. In any event, *Xenoglossa fulva* and species of *Peponapis* appeared to be the most significant agents in the pollination of the cultivated cucurbits growing in the near-by *milpas*. The *Peponapis* was active later in the morning than was *Xenoglossa*.

Male bees were much more numerous at the flowers than were the female bees. Unfortunately it was impossible to study the males' behavior in the predawn period, but brief notes were made on their activity pattern as soon as there was enough light to see them. At that time they were flying from one cucurbit flower to another, occasionally entering unoccupied flowers and moving to the base of the pistil where they frequently remained. If the flowers were occupied, the male *Xenoglossa* entered and approached the other bee regardless of its sex or species. (This same behavior was observed at other localities in Central Mexico.) Later in the morning, the males flew rapidly over and through the vegetative growth of the *Cucurbita*, occasionally stopping to force their way into partially closed flowers.

Xenoglossa fulva Smith² is a very large, robust bee clothed with golden to fulvous pubescence. The ocelli are unusually large, suggesting nocturnal or crepuscular habits. The females produce a low-pitched but loud hum during flight, and can be heard at a distance of 100 feet or more. (In the nest area during the predawn period, this sound appeared to be associated either with straight-line flights at a height of 6 or more feet above ground or with flight close to the ground in search of their burrows.)

²Identified by C. D. Michener, University of Kansas.

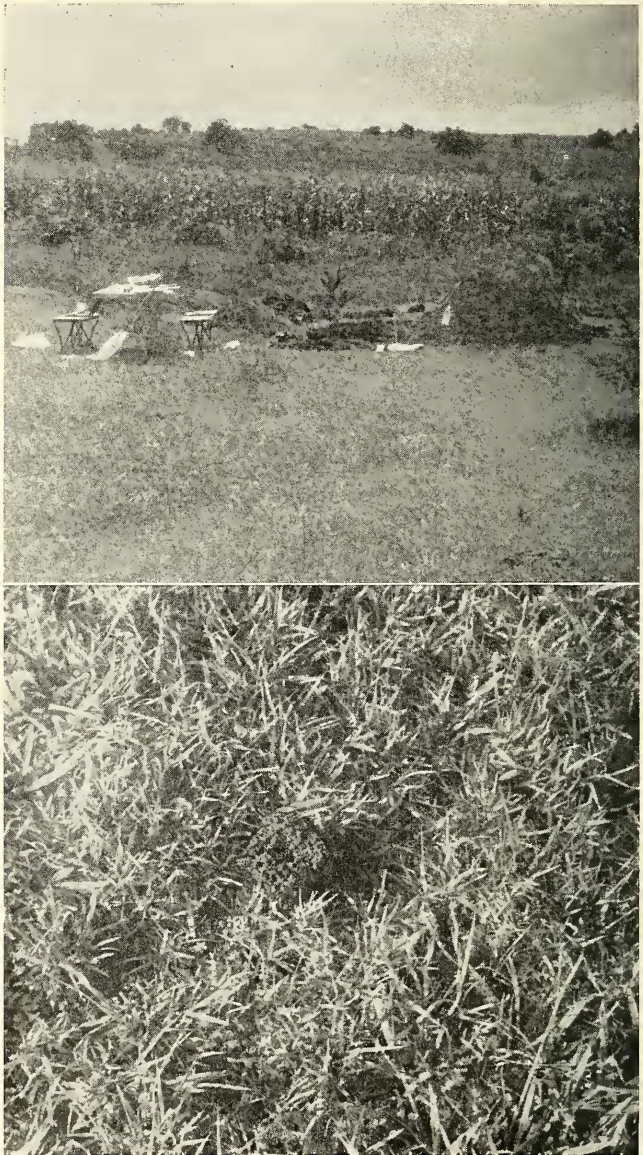


PLATE 36

For explanation of plate, see page 141.

On August 18, before daylight (5:45 a.m.), two females were heard flying outside the tent. Although an observer was stationed within 3 feet of two burrows, it was not until 6:15 a.m. that there was enough light to see a female enter her burrow with a load of pollen. With this lead, other burrows were discovered by daylight, and these were subsequently excavated.³ At 6:20 a.m. a second female returned with a pollen load and, after considerable searching, entered her burrow. At 6:28 a.m. this bee emerged and flew across the arroyo toward the adjacent *milpas*. She returned to her burrow, without pollen, at 12 noon. Bees had been heard in the vicinity of these burrows before 6:15 a.m. on at least five or six occasions, and several prolonged flights suggested that a female might be having difficulty locating her burrow. It would be interesting to know if the females were carrying pollen on these early trips. No females with pollen were seen after 6:20 a.m. Another burrow was located just before 7 a.m., and although a partially provisioned cell was later excavated, this female did not return until after 8 a.m.

On August 19, observations were started at 5 a.m. At 5:25, bees were heard and were seen to visit the flowers of *Salvia amarissima* Ort. It was not possible to catch any of these bees by the light from a flashlight nor to determine definitely that they were *Xenoglossa*. However, by 5:50 a.m. numerous bees could be heard in the area, and at 6:05 a.m. a *Xenoglossa* was identified while taking nectar from *Mandevilla foliosa* (Muell. Arg.) House. At 6:08 a.m. a female with a partial pollen load was observed taking nectar from *Salvia*, and a number of males were also flying around *Salvia*, *Mandevilla*, and *Helmia salicifolia* (HBK) Link. Unfortunately there was little activity around one known and several probable *X. fulva* burrows that had been selected for constant watching. The female from the known burrow left at 5:48 a.m. and, after a few brief flights across the entrance, flew away and had not returned by 8:30 a.m. when the observations were discontinued.

The *Xenoglossa* were nesting in a rather open, grassy area in which there were a few scattered plants of *Acacia* and *Opuntia*. The grass was of several species, coarse and extremely dense (Plate 36, lower fig.), and was kept low by heavy grazing. Pepper trees (*Schinus molle*) and a tree *Ipomea* were common in the vicinity, and in two deep, overgrown arroyos on each side of the nesting site numerous shrubs of *Baccharis* and *Nicotiana* were in bloom.

³Adults, larvae and casts of burrows and cells have been deposited in the collection of the California Insect Survey, University of California, Berkeley, California.

The upper layer of soil was a uniform, dark, mellow clay loam. Mechanical analysis by the pipette method showed sand, 34.6 per cent; silt, 32.0 per cent; and clay, 32.7 per cent. The pH was determined colorimetrically at 6.5. This soil was sufficiently moist, at all levels, to pack into balls, but there was a distinct increase in soil moisture 10 to 20 cm. above the underlying layer of dry, hard-packed adobe. Depth of the surface layer varied from about 50 to 100 cm., as judged from examination of the cliff faces in the arroyos. Toward the southern edge of the grassy area, moderate sized stones were scattered on the surface, but there were few in the nesting area proper, and none was uncovered in the excavation of burrows.

Grass roots formed a thick mat for the first 20 cm., below which occasional large roots of adjacent bushes or trees were encountered. In addition, a few very fine roots were found as deep as 70 cm., but at the lower levels they were not sufficiently abundant to interfere seriously with the nesting activities of the bees.

LIFE HISTORY OBSERVATIONS

OVERWINTERING AND EMERGENCE. During excavation of the burrows, four or five from the previous season were encountered. One such burrow, at a depth of 55 to 60 cm., had four cells, one of which was filled with mud, the adult having emerged. Two cells contained unemerged females, and the fourth, at 60 cm., held a mature, overwintering larva. Another cell associated with an old burrow also contained an unemerged female. Although these cells represent a very small sample from which to draw conclusions, they suggest that *Xenoglossa fulva*, like its relatives, overwinters in the larval stage and transforms shortly before the active season. Furthermore, it would appear that the majority of the males emerge before the females, as evidenced by (1) the large number of males seen in the area; (2) the three unemerged females found in the five cells examined; and (3) the number of emerged females that were just starting burrow excavation. Emergence of the adults appeared to be greatly facilitated by the open condition of a considerable part of the old burrows. The entrances and basal portions of the 1953 burrows were plugged, but large sections of the remainder were open. (In one case, a section 26 cm. in length was unobstructed.)

Since relatively few females were observed at the flowers, it is likely that they start burrow construction almost immediately after emergence.

Mating was not observed, but almost surely occurs in or near the cucurbit flowers, since no males were seen searching the nesting site at any time of day.

NESTING ACTIVITY. The burrows of the 1954 season were in open areas away from bushes or rocks, and were associated with burrows of previous years. Since five of the six active burrows that were found and excavated were widely separated from one another, it seems likely that each female had started her burrow immediately adjacent to the one from which she had emerged. (Association of new and old burrows is apparently common with many species of bees.)

After selecting an acceptable site, the female starts a vertical shaft and pushes the excavated earth to the surface where it accumulates around the entrance. The shape of this tumulus (Plate 36, lower fig.) varied from almost circular to rectangular, due to the configuration of the surrounding terrain, but the entrance was always at or near the center. The height varied from 3 to 6 cm., and the greatest diameter was from 7.5 to 10 cm. One entrance had no tumulus, but since this burrow was later found to be the most advanced in construction, it is probable that earlier rains had washed the tumulus away.

Five burrows were cast in plaster of Paris, and were removed in sections because of their depth. This was accomplished by excavating a deep hole (Plate 36, upper fig.) about 18 inches away from the burrow and removing blocks of earth from which the cast was carefully dissected. The vertical depth of the burrow was measured in each block before dissection in order to determine the total vertical depth as contrasted with the length of the burrow. For example, the burrow illustrated in Plate 2, figure 1, had a vertical depth of 70 cm. and a linear measurement (main shaft) of 88.5 cm.

All burrows showed many minor deviations from the vertical not associated with irregularities in the soil, one or more blind branches, one or more nearly horizontal turns and vertical ends. The numerous curvatures gave a somewhat spiral shape to the main burrow shaft. The diameters of the individual burrows, exclusive of the portion just before the cell, varied from as narrow as 10.5 mm. to a more typical range between 12 and 14 mm. The walls of the main shaft were slightly rough, but showed no evidence of use of the pygidium in burrow construction.⁴ About 4 cm. above the entrance to a cell the wall became smooth, and the diameter was reduced in the last two centimeters from about 12 to 9 mm.

Two of the five burrows were still in process of construction. One of them extended to a vertical depth of 76 cm., the other to about 80 cm. Of the other three burrows, two terminated

⁴The authors have excavated casts of burrows of *Andrena perimelas* Cockerell, which also constructs large, deep burrows in comparable soil types, and have found numerous raised casts of the pygidium, indicating that it is used in packing the walls of the burrows in this species.

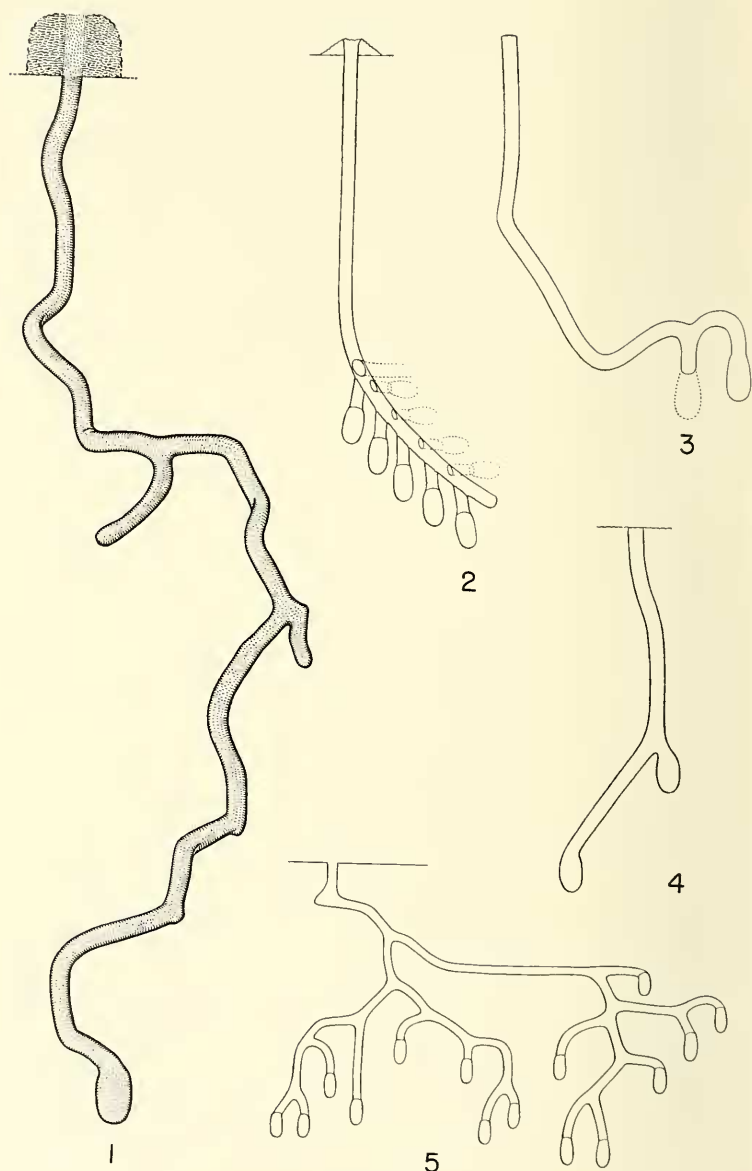


PLATE 37

For explanation of figures, see page 141.

in single cells with pollen, and the third terminated in two cells—one containing pollen and the other, a first instar larva. The newer of these two cells was at a depth of 63 cm., and 2 cm. to the side of the completed cell which was at a depth of 64.5 cm. The cells in the other two burrows were at depths of 56.5 and 63 cm., respectively. Three cells from the previous season were measured at depths of 56 to 58.5 cm. All of the cells were within 3 to 10 cm. of the layer of dry, hard-packed adobe. In one case, a burrow terminated at a greater depth (70 cm.) than that of the cell associated with it (63 cm.).

Xenoglossa fulva constructs a cavity in the soil and smooths and lines it to form a cell. Microscopic examination failed to reveal any difference in texture between the soil adjacent to the lined cavity and that half an inch distant. The absence of an outer cell wall made excavation very difficult, and the cells could not be recognized until they were damaged or cut open.

The shape of the interior of the cell differs from that of many anthophorids in that the anterior portion is not conspicuously narrowed; the apical half is almost parallel-sided; and the walls of the basal half are slightly bulged. The inner surface is smooth, and covered with a thin coat of waterproof lining material.

Pollen loads are placed at the bottom of the cell and later are evenly packed. Although the amount of pollen was not accurately measured, it filled only about one-fourth or one-fifth of the cell. The completed pollen mass was covered with a thin layer of nectar which lacked the strong fermented odor so characteristic of *Anthophora*. In one cell, a first instar larva was floating on the liquid, with its head near the cell wall. Thus it may be that the egg is floated in the center of the liquids as with the Anthophorinae.

Something of the development and activities within the cell was reconstructed from an examination of the cells from the 1953 season. Dissection of a cell containing a mature larva showed that it had defecated prior to forming a cocoon. Following or in the process of defecation, the relatively small amount of fecal material is worked to the upper end of the cell. This movement is possibly synchronized with the first silk production since the fecal material occurs between the cell wall and the upper, somewhat mammiform top of the cocoon (Plate 38, fig. 2). The apical, cap-like portion is formed of about six layers of dark and coarsely woven silk fibers, and is approximately 12 mm. wide at the base. The layers of silk are compacted near the margins, but are separated from each other near the center. Beneath these coarse silk layers is a median circular mat of light brown silk, slightly curved, and measuring about 7 mm. in diameter.

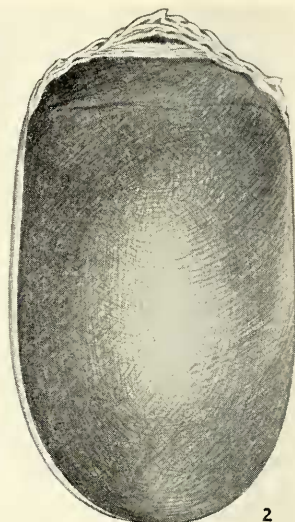


PLATE 38

For explanation of figures, see page 141.

This mat is also composed of a number of distinct silken layers. One mat was dissected and 20 complete layers were separated. Both the apical cap and the mat are composed largely of fibers and are somewhat dull. The other walls of the cocoon are made up of thin layers which contain no free silk strands and only a few strand-like markings. On separation, these layers have a metallic sheen which is somewhat less evident on the innermost surface. The outer layer is deposited directly on the cell wall and this lining adheres to the cocoon when it is removed from the cell wall and this lining adheres to the cocoon when it is removed from the cell. Although the wall of the cocoon is composed of several layers, it is thin and parchment-like, and dents at the slightest pressure. The larva presumably overwinters within the cocoon, and pupation probably follows in late June, July, or August.

No parasites were clearly associated with *X. fulva*. However, several females of *Pseudomethoca ravula* (Cameron)⁵ were taken searching over the nesting area, and three additional females were found in the earth removed during excavation of fresh burrows. Whether these females were emerging from cells of the previous season or had taken shelter in old burrows is problematical. Unfortunately no cells containing mutillids or their cocoons were uncovered. Nevertheless, the large size of the individuals of *P. ravula* suggests a host-parasite relationship with *X. fulva*.

BIOLOGICAL CHARACTERS OF THE EUCERINI

A comparison of the habits of *Xenoglossa* with those of other Eucerine bees (as defined by Michener, 1944) reveals a number of similarities that permit a tentative tribal characterization on biological grounds. However, information on the genera *Melissodes*, *Tetralonia*, and *Eucera* is incomplete, and is nearly or completely lacking for the Old World genera *Tetraloniella*, *Eucara*, *Melissina*, *Thygatina* and the New World genera *Eclectica*, *Holmbergiapis*, *Melissoptila*, *Scastra*, *Thygater*, *Thyreothremma*, *Cemolobus*, *Peponapis*, *Anthedonia*, *Martinapis*, *Florilegus*, *Xenoglossodes*, *Nectarodiaeta*, and *Canephorula*. Although this represents a large number of genera, the majority are presumed to be close relatives of one or another of the four genera here discussed. In this account we have drawn upon unpublished observations on the habits of three species of *Melissodes*, two species of *Tetralonia*, and one species of *Xenoglossodes*, supplemented from published accounts of the habits of several species of *Eucera*, *Melissodes*, and *Tetralonia*.

⁵Identified by P. D. Hurd, University of California, Berkeley

Although the number of references on the flower and nesting habits of various species of *Eucera*, *Tetralonia*, and *Melissodes* is considerable, only a few papers were found to contain sufficient textual and illustrative material to serve for comparative purposes. Malyshev's (1929) summary of the biology of *Tetralonia malvae* Rossi contains information from his earlier papers together with new and excellent illustrations. Similarly, Friese's (1923) treatment of *Eucera difficilis* Perez contains the clearest illustration of the burrow of this species as well as a verbatim account of Fahringer's paper on *Tetralonia nana* Mor. Custer's (1928, 1929) reports on the habits of *Melissodes obliqua* (Say), and Hicks' (1936) note on the burrow pattern of *Melissodes timberlakei* Ckll., have also furnished useful information for comparison.

The burrows of only a few Eucerine bees have been described or figured (Plate 2) yet considerable variation in their location and structure is evident. The known species use flat to steeply sloping ground either with or without a vegetative cover, although none has been recorded nesting in vertical banks. Each species appears to select characteristic nest sites. The depths of the burrows vary from 8 or 10 cm. (*Melissodes timberlakei* Ckll.) to about 80 cm. (*Xenoglossa fulva* Smith). All of the burrows previously described, as well as those investigated by the authors, have the entrance shaft vertical and the main tunnel somewhat sinuous. Only species of *Eucera* have been recorded as constructing turrets at the burrow entrance in the manner of the Emphorinae and some *Anthophora*.

The most striking characteristic of the burrow structure in most species is in the individual placement of the cells and their vertical orientation. The isolation of the cells is usually considered a characteristic of most Andrenidae and Halictidae. Most other anthophorid bees arrange the cells serially. The vertical placement of each cell appears to be found in all of the known Eucerini with the possible exceptions of *Eucera difficilis* Perez and *Tetralonia nana* Mor. In the case of *E. difficilis*, the authors have been unable to interpret fully the illustration given by Friese (1923) and reproduced diagrammatically (Pl. 37, fig. 2). In this diagram the series of cells shown by dotted lines are not vertical, and there is no clarifying information in the text. Fahringer's (1914) illustration of the burrow of *Tetralonia nana* Mor. shows most of the cells to be almost horizontal, in striking contrast to the vertical cells of *T. malvae*, as illustrated by Malyshev (1929). The vertical orientation of the cells is probably associated with the partially liquid or semiliquid nature of part of the provisions. In the genus *Anthophora* many species make vertical cells and provision them first with pollen and then with a surface layer of liquid. However, in Central Mexico, a species of *Micranthophora* placed its cells at a 60° angle to the vertical and provisioned a very moist pollen

mass. Although *X. fulva* did not appear to construct a cell within a cavity, as is common with most anthophorid bees, it is assumed that this may have been due to the nature of the soil in the particular site. A similar situation was found for *Melissodes robustior* Ckll. when its burrows were excavated from a fine, moist, clay soil. Fahringer (1914) also failed to find recognizable cells in his studies of *Tetralonia nana* Mor.

The internal shape of the cells of Eucerine bees appears to be uniform, and is distinctive from those of the Emphorine and Anthophorine bees. In the former, the shape is elongate oval; in the latter it is more urn-shaped.

The cells of most if not all species of the Anthophoridae have a wax-like inner lining. This lining is thick in the species of *Anthophora* and very thin in the Emphorini and Eucerini.

The pollen preferences of many species of the Anthophoridae have been published, and this aspect of the habits of these bees is better known than are others. The members of the Emphorinae and Eucerinae are largely oligolectic, while the majority of the species of Anthophorinae are polylectic. However, all species visit a wide variety of flowers for nectar.

Eucera difficilis Perez works the food materials into a ball upon which the egg is placed. The known species of *Tetralonia*, *Melissodes*, and *Xenoglossa* pack the pollen into the base of the cell and cover it with a thin layer of nectar, which may be mixed partially with the surface pollen. According to Malyshev (1929), the curved eggs of *Tetralonia malvae* Rossi and *T. dentata* Klg. are placed in the center of the cells with both ends inserted into this semiliquid material. The volume of liquid in the cell of *X. fulva* has been interpreted as indicating that the egg is floated on the food mass. The liquid provisioned by species of *Tetralonia*, *Melissodes*, and *Xenoglossa* does not have the strong fermenting odor which we have found to be characteristic of *Anthophora* and *Micranthophora*. Similarly, the cells of *Diadasia*, *Melitoma*, and *Ptilothrix*, the species of which place a pollen mass, with little or no nectar, on top of the egg, had no such fermenting odor.

The fecal material, which is produced following larval feeding, is distributed in a variety of ways. The larvae of the anthophorines and of *Eucera* defecate a semiliquid material in the bottom of the cell. Emphorine larvae distribute their fecal material in a thin, uniform layer over the entire inner cell surface. *Tetralonia malvae*, *X. fulva*, and a number of species of *Melissodes* place their fecal material at the upper end of the cell. *Melissodes robustior* Ckll. manipulates it in a complex and uniform pattern (Plate 38, fig. 3).

Cocoon formation follows defecation in Emphorine and Eu-

cerine bees. In the former, the cocoon is a thin, varnish-like layer separating the larva from the fecal material, and in the latter, it is a distinct, double-walled cocoon. Species of *Eucera* construct a cocoon of uniform thickness while those of *Tetralonia*, *Melissodes*, and *Xenoglossa* prepare a cocoon which contains many more layers of silk at the upper end. The cocoon of *X. fulva* is the most complex of those now known, and has been described above in detail.

There appears to be no evidence, among the Eucerine bees, of the gregarious habit recorded for many species of Anthophorinae and for *Melitoma* (Emphorinae).

Conclusions: From the above it appears that the Eucerinae may be defined by the following biological characteristics: oligolecty, solitary nesting habits, oval-shaped cells, solitary cells, thin cell linings, eggs on top of provisions, and double-walled cocoons. The Emphorinae, as now defined (Linsley, MacSwain, and Smith, 1952), are similar in oligolecty, thin cell linings, and production of larval silk, but differ in having a greater gregariousness, urn-shaped cells, eggs under the food masses, the application of the larval feces on the cell walls, and single-walled cocoons. The Emphorinae are somewhat intermediate in the orientation of the cells, and the known species of *Diadasia* and *Melitoma* construct cells in series, *Emphor* and *Ptilothrix*, isolated. The Anthophorinae, while sharing more characteristics with the Emphorinae, are separable from both the Eucerinae and Emphorinae by the strong, fermenting liquids in the cells and the thick, wax-like cell linings.

Within the Eucerinae, the species of the genus *Eucera* exhibit a number of primitive characters, such as a round pollen ball with the egg attached, larval excrement at the bottom of the cell, and a uniformly woven cocoon. No interpretation has been made of the close approximation of the cells or their apparent deviation from a vertical position, and these same features are apparently shared by *Tetralonia nana*. The formation of a turret at the entrance of the burrows of species of *Eucera* is a specialization.

Tetralonia malvae, the known species of *Melissodes*, and *Xenoglossa fulva* share the following specialized characteristics: Cells vertical, pollen packed into base of cells, liquid layer covering pollen masses, larval excrement placed at cell entrances, and tops, of cocoons constructed of a number of coarse and fine layers of silk. The construction of the upper portion of the cocoon is most complex for *X. fulva*. It is suggested, on biological grounds, that the species of *Eucera* are closest to the ancestral stock of the Eucerinae, those of *Tetralonia* probably next, those of *Melissodes* more distant, and finally the genus *Xenoglossa* as a specialized offshoot related to *Melissodes*.

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EXPLANATION OF PLATES

- Plate 36. Upper figure, nesting site of *Xenoglossa fulva* Smith with excavation in center and *milpa* in background. Lower figure, tumulus of *X. fulva*.
- Plate 37. Burrow diagrams of Eucerine bees. Figure 1, *Xenoglossa fulva* Smith (orig). Figure 2, *Eucera difficilis* Perez (after Friese, 1923). Figure 3, *Tetralonia malvae* Rossi (after Malyshev, 1929). Figure 4, *Melissodes* sp. (orig.). Figure 5, *Melissodes obliqua* (Say) (after Custer, 1928).
- Plate 38. Cocoons. Figure 1, *Xenoglossa fulva* Smith, external view with excrement removed. Figure 2, *X. fulva*, longitudinal section with excrement removed. Figure 3, *Melissodes robustior* Ckll., with excrement in place. Figure 4, *M. robustior*, longitudinal section with excrement removed.

